ON THE PROBLEM OF IDENTIFYING HOMOLOGIES IN LITHIC ARTIFACTS

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RESUMEN

Homología es un concepto fundamental en las ciencias históricas, es decir, en aquellos campos disciplinarios orientados a explicar los fenómenos naturales en términos de causas que operaron en el pasado. En arqueología, el interés por el reconocimiento de las homologías se ha incrementado notoriamente en los últimos años bajo la influencia del paradigma evolutivo. En este campo de investigación, el enfoque predominante para el tratamiento de las homologías está basado en la aplicación de la metodología cladística. Como consecuencia de ello, el concepto de homología subyacente en la mayoría de los estudios filogenéticos actuales es un concepto estrecho, casi exclusivamente basado sobre el criterio de similitud. El objetivo de este trabajo es poner de relieve la necesidad de ampliar el marco para la formulación y puesta a prueba de hipótesis de homología dentro del campo de la arqueología evolutiva mediante la adopción de una perspectiva basada en el estudio de las trayectorias ontogenéticas de los artefactos, tanto sobre una base individual como poblacional. Se concluye que el éxito de este enfoque depende, en gran medida, de la adquisición de un conocimiento detallado acerca de la influencia relativa, sobre los patrones de variación morfológica, de factores que controlan la ontogenia de los fenotipos artefactuales, i.e. la homeostasis del desarrollo (a través de la canalización o de la estabilidad del desarrollo) *vs.* la plasticidad fenotípica. Estos y otros temas estrechamente relacionados entre sí, tales como la evaluación y la cuantificación de la contribución relativa de la información culturalmente heredada y cognitivamente procesada y del ambiente sobre la constitución de los fenotipos artefactuales, deben integrar una agenda para el trabajo futuro sobre este tema.

Palabras Clave: homología, artefactos líticos, ontogenia, experimentación replicativa

ABSTRACT

Homology is a fundamental concept in historical sciences, i.e. those disciplinary fields aimed at explaining natural phenomena in terms of causes that operated in the deep past. In archaeology, the interest for homology recognition has notoriously increased in recent years under the influence of the evolutionary paradigm. In this field of inquiry, the prevailing approach to homology is one based on the cladistic methodology. As a consequence, the homology concept lying behind most of the current phylogenetic studies on artifacts, including lithics, is a narrow one almost exclusively based on the similarity criterion. The aim of this paper is to underscore the need to enlarge the framework for homology recognition and testing in evolutionary archaeology by adopting a developmental perspective, based on the study of ontogenetic trajectories of artifacts on an individual and population basis. It is argued that the success of such an approach is highly dependent on the acquisition of a detailed knowledge about the relative contribution, on morphological variation patterns, of factors controlling the ontogeny of artifactual phenotypes, i.e. developmental homeostasis (through canalization or developmental stability) vs. phenotypic plasticity. These and closely related issues, like the assessing and quantification of the relative contribution of informational and environmental factors to the constitution of artifactual phenotypes, should integrate an agenda for future work on this topic.

Keywords: homology, lithic artifacts, ontogeny, replicative experimentation

INTRODUCTION

Homology is a central notion in historical sciences (Bigandt and Griffiths 2007), i.e. those disciplinary fields aimed at explaining natural phenomena in terms of long past causes (Cleland 2002). The anthropological and archaeological concern for reliability in homology identification, particularly in the context of distinguishing between homologous

and analogous cultural similarities, has a very long history indeed (e.g., Galton 1889; Kroeber 1931; Binford 1968; Clarke 1968; O'Brien and Lyman 2000; Hodder 2001; see O'Brien 2010: 313-317). In fact, the clear distinction between homology and nonhomology (i.e. analogy, homoplasy) is a very important archaeological matter—despite of the archaeologist's paradigmatic orientation or bias, as Hodder (2001: 85) nicely reminds us—whenever we are interested in establishing historical connections between facts concerning past human behaviour. Moreover, in any attempt to investigate evolutionary relationships—both phylogenetic and ontogenetic—between and among artifactual phenotypes of any class (e.g., Foley 1987; Collard and Shennan 2000; O'Brien *et al.* 2001, 2002; Tehrani and Collard 2002; Jordan and Shennan 2003; O'Brien and Lyman 2003; Shennan and Collard 2005; Darwent and O'Brien 2005; Eerkens *et al.* 2005; Jordan and Mace 2005; Buchanan and Collard 2007, 2008; Riede 2009; Lycett 2010), such a distinction is not only desirable but crucial. In view of its importance, it is surprising that the identification of homologies in artifacts currently constitutes a rather underdeveloped area of archaeological inquiry (cf. O'Brien 2010: 327).

The idea advanced in this paper is that the homology concept lying behind most of the current phylogenetic studies on artifacts, including lithics, is a narrow one almost exclusively based on a similarity criterion (e.g., Lycett 2007: 544). This can be considered as the logical outcome of the cladistic methodology adopted by many of such phylogenetic studies (e.g., O'Brien *et al.* 2001, 2002; O'Brien and Lyman 2003; Buchanan and Collard 2007, 2008; Riede 2009; Scheinsohn 2009; Scheinsohn *et al.* 2009; Lycett 2010), which stresses the equivalence between homologies and synapomorphies (Patterson 1982; de Pinna 1991), and the adoption of a posterior homology assessment approach (Kleisner 2007) that uses inferred phylogenetic relationships to test homology hypotheses based on inferred monophyletic groups after the application of parsimony and congruence criteria (Patterson 1982, 1988; de Pinna 1991; Haszprunar 1992; Brower and Schawaroch 1996; Sluys 1996). Under this approach, homology becomes the end-product of a phylogenetic analysis rather than something that needs to be thoroughly investigated—using a variety of criteria like comparative morphological studies, topology, connectivity, ontogeny, and functional anatomy (Kearney and Rieppel 2006)—before (or besides) cladogram construction and evaluation. An obvious consequence of this practice is that many potentially important and useful homologous characters not similar in position, structure, or function tend to remain virtually undetectable.

My aim is not so much to criticize the assumptions and methodology of current phylogenetic studies on material culture as to underscore the need to enlarge the framework for homology recognition and testing in evolutionary archaeology. This goal is in line with recent claims in systematics and philosophy of biology which advocate for at least some causal grounding for homology hypotheses beyond mere congruence (Rieppel and Kearney 2002; Kearney and Rieppel 2006; Love 2007; Winther 2009; Assis and Rieppel 2011), as well as with the main tenets of the emerging research program that is looking for a unified approach to homology through the coherent integration of ontogeny and phylogeny (Laubichler 2000; Rieppel 2005; Wagner 2007; Wagner *et al.* 2007; Ereshefsky 2009). In order to achieve the proposed aim I will: (1) briefly review the current literature about the meaning of homology in evolutionary biology and the different available criteria to recognize homologous characters, (2) present and discuss the assessment criteria for homologies used by most of the phylogenetic studies on artifactual variation carried out over the last 10 years, (3) propose complementary ways of searching for homologies in artifacts, highlighting the advantages and problems associated with their implementation, and (4) sketch the lines of research that would be beneficially explored in order to gain knowledge about patterns of artifactual variation and about the mechanisms involved in the evolution—both ontogenetic and phylogenetic—of the artifactual phenotypes.

THE MEANING OF HOMOLOGY IN EVOLUTIONARY BIOLOGY AND THE DIFFERENT WAYS OF IDENTIFYING HOMOLOGOUS CHARACTERS

To try to summarize all the points of contention in the current debate surrounding the

homology concept(s) is a very difficult task, due to the inherent complexity of the subject matter and to the considerable bulk of literature on the issue that has been produced in recent years (for comprehensive and critical reviews see, among others, Patterson 1982; Rieppel 1988; Donoghue 1992; Hall 1994, 2003; Lauder 1994; Bock and Cardew 1999; Brower 2000; Brigandt 2003; Cracraft 2005; Kearney and Rieppel 2006; Griffiths 2007; Kleisner 2007; Wake 2003; Ereshefsky 2009). In this section I will only concentrate on those aspects relevant to my discussion, namely the restriction of the meaning of homology operated in cladistics—with all its conceptual and practical consequences—, and the theoretical and methodological alternatives existing today in evolutionary biology to tackle the problem of homology recognition.

Among the many conceptualizations of homology proposed during the last five decades, the two most widely accepted nowadays are the taxic and the developmental approaches (Griffiths 2006; Kleisner 2007; Ereshefsky 2009). In the taxic conception, which was embraced by the so-called pattern or transformed cladistics (*sensu* Beatty 1982) or, more simply, Cladistics (with a capital C; Williams *et al.* 2008: 85) over the last 30 years, characters in different taxa are homologous if those taxa possess the character by descent from a common ancestor (Griffiths 2007), thus implying a hierarchy of groups and the formulation of hypotheses of monophyly (Patterson 1982, 1988; Stevens 1984; de Pinna 1991). For the developmental approach, two characters are homologous if they share the same set of developmental constraints (Wagner 1989a), which conforms a developmental module causing the stable production of a homologue (Wagner 1996). Such developmental module would consist of a gene regulatory network composed by the genes and their corresponding interactions (Abouheif 1999; Bolker 2000; Wagner 2007; Wagner *et al.* 2007; Kuratani 2009).

The taxic approach to homology has its formal origins in the work of Patterson (1982), who draws on the distinction made by Eldredge (1979) between taxic and transformational approaches to process analysis in evolution. Patterson (1982), following the propositions of several authors (e.g., Wiley 1975, 1976; Bonde 1977; Platnick and Cameron 1977; Szalay 1977; Cracraft 1978; Nelson 1978; Gaffney 1979; Platnick 1979; Eldredge and Cracraft 1980; Nelson and Platnick 1981; see discussion in de Pinna 1991), explicitly established an equivalence in meaning between homology and synapomorphy (i.e. a derived or specialized character shared by two or more taxa that originated in their last common ancestor), which is a fundamental concept in the logical framework of cladistics. The proposed equivalence was explicitly acknowledged by Nelson and Platnick (1981: 137) and de Pinna (1991: 369) as a restriction in the meaning of the term 'homology', whose philosophical justification resides in the fact that such restriction implies a greater logical specificity and a greater empirical content of the concept, and hence an increased scientific value. From a methodological standpoint, de Pinna (1991: 371) states that "by equating all derived similarities with synapomorphy, it is possible to detect a common pattern of internested attributes". It is precisely under such framework, which operationally makes all characters equivalent to hypothesized synapomorphies, that the procedure of finding out a common pattern among taxa can be performed (de Pinna 1991).

In the taxic approach that pervades current cladistics, a homology—considered as a mental construct or abstraction (Patterson 1982, 1988, Nelson 1989; see discussion in Kleisner 2007: 328)—has always the status of a hypothesis. In consequence, the main effort is put in the process of hypothesis testing, which can be accomplished with the aid of the three tests proposed by Patterson (1982): similarity, conjunction, and congruence. It is intended that the results of these tests can discriminate different categories of homology and homoplasy (nonhomology) (Patterson 1988: 604). For Patterson (1982, 1988), similarity—concerning topographic, histological, developmental, and compositional attributes—is deemed the traditional criterion of comparative morphology. Since nonhomology also implies similarity, it is considered an insufficient and weak tool to tests a hypothesis of homology, but useful enough to validate a hypothesized homology as worthy of further examination because, as Cracraft (1981: 25) rightly pointed out, "similarity is the factor that compels us to postulate homology" (see also Stevens 1984: 403). Conjunction, devised by Patterson (1982) as a test capable of disproving

homologies as anatomical singulars, excludes the presence of two homologues within a single organism, i.e. if two putative homologues are found together in one organism, they logically cannot be homologous (Rose and Lauder 1996). Congruence, finally, is considered the most decisive test of homology (Patterson 1988: 605). It depends on the equivalence between homology and synapomorphy, and is based on the principle of parsimony (Patterson 1982: 38). In testing a hypothesis of homology by congruence, the distribution of the target feature is confronted against the distribution of other putative homologies: a proper homology will define a group that is congruent with those specified by other homologies. Comparatively, then, congruence test is the most powerful of the three assessment procedures proposed by Patterson (1982), and purportedly the only one capable of accurately discriminate between homology and homoplasy.

In summary, it can be said that the taxic definition of homology attaches great importance to the systematic requirement for monophyletic trees, adjudicating a minor or a secondary significance to anatomical and developmental facts like position or embryological origin (Amundson 2001). Under the taxic approach adopted by cladistics, the determination of homologies takes the form of a at least two-step procedure (cf. Brower and Schawaroch 1996): the first step consists in the identification of a putative, i.e. hypothetical, homology between characters or character states present in two or more taxa (primary homology, *sensu* de Pinna 1991), which is inferred on the basis of some a priori criteria, mainly similarity; the second step consists in the testing of the homology hypothesis by means of a phylogenetic analysis based on the principles of congruence and parsimony. The homology propositions that successfully pass such tests are then called secondary homologies or synapomorphies (de Pinna 1991).

In opposition to the taxic approach, the developmental stance to homology centres its attention on ontogeny rather than on phylogeny (Ereshefsky 2009). As presented by Wagner (1989a, 1989b, 1999), the so-called 'biological homology concept' emerged within this framework as an approach to homology interested in generative biological mechanisms (i.e. processes) rather than in purely genealogical relations.

Starting from the premise that homology is a relation between parts of the body and drawing on ideas contained in the work of Roth (1984) and of early and middle 20th Century biologists like H. Spemann, F. Baltzer and H. Kroeger, Wagner (1989a: 62) provided a preliminary definition of biological homology which states that

"Structures from two individuals or from the same individual are homologous if they share a set of developmental constraints, caused by locally acting self-regulatory mechanisms of organ differentiation. These structures are thus developmentally individualized parts of the phenotype."

It is followed from this definition that the homology relation cannot be meaningfully predicated of all conceivable features, but only of those developmentally constrained morphological patterns (Wagner 1989a: 66).

Wagner (1989b) considers that the research program on the biological basis of homology should approach the evolution of morphological characters at two different levels. The first one refers to character modification within a definite framework of developmental constraints, whereas the second one refers to the evolutionary modifications of such constraints. The need to deal with the problem of homology at two different levels has also been acknowledged by Laubichler (2000), who argues that homology should be explained with reference to both, development and (phylogenetic) evolution, since development is the proximate cause of morphological characters and phylogenetic evolution implies either organic transformation or stability.

Functional to the growth of the developmental approach to homology—and to the entire field of evolutionary development or 'evo-devo'—has been the view, adopted by many during the last 15 years, that morphological characters at the organismic level may be considered the phenotypic units of evolutionary transformation, units that can be meaningfully compared more or less independently one from another in an interspecific context (Wagner 1996). Such units are called modules (Wagner 1996; Raff 1996; Carroll *et al.* 2001; Schlosser and Wagner 2004; Wagnet *et al.* 2007; Klingenberg, 2008; Kuratani 2009), and it is

intended that they conceptually fill the gap between genes and phenotypes by providing a possible link between both domains (Kuratani 2009: 61). In this connection, different authors have proposed that the developmental modules, considered as units of evolvability (Laubichler 2000; Brigandt 2007; cf. Ereshevsky 2009), consist of a gene regulatory network composed by the genes and their respective interactions (Abouheif 1999; Bolker 2000; Wagner 2007; Wagner *et al.* 2007; Kuratani 2009).

Within the framework of the developmental approach to homology, Wagner (1999: 125) has stipulated a research program for testing the biological homology concept based on a combination of comparative, genealogical, and experimental methods. Such research program entails the following steps:

"(1) identifying of two or more putative homologues in a clade; (2) determining the phylogenetic distribution of the putative homologues; (3) describing the intra- and interspecific variation patterns of each putative homologue; (4) describing the development of each putative homologue, and determining if modes of development and distribution of homologues are phylogenetically congruent; and (5) providing and testing a model of how differences in modes of development between putative homologues effect differences in variational tendencies."

As it has been widely debated (e.g., Roth 1988; Brigandt 2002, 2003, 2007, 2008; Hall 2003, 2007; Wake 2003; Grant y Kluge 2004; Cracraft 2005; Ghiselin 2005; Kearney and Rieppel 2006; Griffiths 2006, 2007; Bigandt and Griffiths 2007; Kearney 2007; Kleisner 2007; Rieppel and Kearney 2007; Matthen 2007; Winther 2009; Assis and Rieppel 2011), the taxic and developmental approaches to homology definition and recognition are source of both enlightenment and shortcomings depending on the application context. In part to overcome this situation, some scholars are now advocating for a unified approach to homology, one that coherently integrates ontogeny and phylogeny into a single operative framework (Laubichler 2000; Rieppel 2005; Wagner 2007; Ereshefsky 2009). Recently, Ereshevsky (2009) has given an account of the rationale for such integration that is based on three affirmations: (1) *phylogeny is essential for establishing the identity conditions of a homologous character*; (2) *ontogeny is essential for explaining variation and similarity among the character states of a homologue*; and (3) *developmental factors need to be transmitted across generations*. The success of this ongoing undertaking remains to be judged [for a pessimistic view about this whole enterprise, see Maynard-Smith (quoted in Tautz 1998: 17); Wake (2003); Griffiths (2007)], but the logic behind the effort is certainly sound.

From the precedent review it becomes clear that for to get a deeper understanding of evolution occurring at different levels along a hierarchy of entities and processes, there is an urgent need of integrating pattern and process in a coherent way. In this endeavour, the role of homology as a pivotal concept cannot be overemphasized. This alone justifies the importance of reaching a trade-off between specificity and generality in homology definition, and of developing an integrated and coherent methodological approach for homology recognition and testing. This is something that is valid for biology and for archaeology as well.

THE TREATMENT OF HOMOLOGY IN EVOLUTIONARY ARCHAEOLOGY: A CRITICAL APPRAISAL

As stated above, the prevailing approach in evolutionary archaeology to the homology identification problem is one based on the cladistic methodology. The rationale behind this fact resides in the current emphasis on phylogenetic reconstruction (i.e. what causes what and in what order; O'Brien and Lyman 2003) as a way to tackle the issue of cultural transmission and artifactual evolution (i.e. if things evolve in a nonrandom way, they can be properly studied by the use of cladistics; O'Brien and Lyman 2003). In this context and as long as cladistics became the most commonly used phylogenetic methodology in biological systematics over recent decades, most evolutionary-oriented archaeologists adopted it in order to investigate historical connections concerning artifactual data (e.g., O'Brien *et al.* 2001; Lyman and O'Brien 2005; contributions in O'Brien 2008; Lycett 2010). As a consequence, cladistics virtually replaced seriation, which was the preferred approach in

evolutionary archaeology in its early days (Dunnell 1970; Teltser 1995; Lyman *et al.* 1998).

As depicted by Buchanan and Collard (2007: 368) and Lycett (2007: 544; 2010: 210-211), archaeological applications of cladistics proceed along the same series of steps used in biological systematics (McLennan and Brooks 2001). Under this approach, homologies are considered as hypotheses about historical relationship between characters or character states present in two or more analytical units referred to as Operative Taxonomic Units (OTUs). Such hypotheses are mainly formulated on the basis of a similarity criterion and are tested by means of the inferred phylogenetic relationships after analysis completion (Lycett 2007: 544) (i.e. posterior homology assessment approach; *sensu* Kleisner 2007).

It is important to note that archaeological cladistics uses both qualitative and quantitative (morphometric) data, either separately or in combination (e.g., O'Brien *et al.* 2001; Buchanan and Collard 2007, 2008; Lycett 2009a, 2009b, 2010). In morphometrics, particularly in landmark or geometric morphometrics, 'homology' primarily refers to "correspondence of point(s) (or measurement) across the range of lithic forms in a given analysis" (Lycett 2009a: 88), not necessarily implying "common evolutionary (i.e. genealogical) ancestry and/or common developmental pathways" (Lycett 2009a: 88; see also Buchanan *et al.* 2007: 284-285, and Lycett and Chauhan 2010: 16-18). It is worth reminding that the primary concern of morphometrics is to ensure comparability between cases in form (both, shape and size) analysis in order to proportionate meaningful information about variation within a collection of specimens, and not strictly to reveal or assess genealogical relationships (O'Higgins 2000: 105). In fact, the degree to which either 2D or 3D landmark configurations or even distances between points sampled from a biological form relate to truly homologous structures is, usually, difficult to estimate owing to the allowed combination, in geometric morphometrics, of different kinds of reference points (i.e. Type I, Type II, and Type III landmarks; Bookstein 1991, 1997), each of them carrying a distinct 'homology signal' (see discussion in Cardillo 2010: 327-328). Nevertheless, if each point is clearly defined and consistently identified, the comparability of landmark configurations or measurements between specimens in a sample is guaranteed. In any case, it is clear that in morphometrics—like in cladistics—homology claims always adopt the form of a priori putative statements (O'Higgins 2000: 106; Strauss 2010: 73), which, in this case, remain basically untested throughout the entire analysis.

Two main criticisms can be raised against the widespread treatment of the homology problem in evolutionary archaeology, at least as it was succinctly reviewed here. The first one refers to the use of the similarity criterion as the only source of hypotheses about homology. The second one refers to the current lack of emphasis on the development of a sound methodology for detailed character analysis in order to independently test homology assertions, as well as to discover unexpected homologous relationships between morphological traits.

Despite the fact that morphological similarity—i.e. the extent to which one form resembles another form, as determined according to some specified set of criteria and procedures—is often considered the prerequisite of a homology hypothesis (Cracraft 1981: 25; Stevens 1984: 403), and even "the very phenomenon that the systematic method is supposed to account for" (de Pinna 1991: 377), it is clear that traits similar in terms of size, shape or function may be non-homologues and traits dissimilar in terms of such properties may be homologues (Rieppel and Kearney 2002: 63). Indeed, morphological similarity as a criterion for homology identification may be potentially misleading due to the fact that evolutionary modifications can cause a loss of morphological resemblance of homologous structures, while reasons other than common ancestry (e.g., convergent evolution) can make two non-homologous structures appear quite similar thus complicating the recognition of truly homologous structures (Lao and Tomoyasu 2011: 232).

It is relevant to introduce here the key distinction between the terms 'similarity' and 'sameness'. To put it simply, homology is a relation of sameness not similarity (Müller 2003; Ghiselin 2005; Ereshefsky 2009). Sameness, the quality or condition of being the

same or identical (Noonan 2009), was first brought in by Owen (1843) as the criterion to distinguish between homology, i.e. the presence of the same parts in every variety of form and function, and analogy, i.e. similarity of parts in their functional adaptations. As it is understood, structures in different taxa are proposed to be homologous only if it is thought that the *same* structures—in some specified sense—were present in their common ancestor, irrespective of their degree of similarity or resemblance (Puelles and Medina 2002: 243). From a logical point of view, we can have sameness with similarity (homology), sameness without similarity (homology), and similarity without sameness (analogy, homoplasy). It follows that similarity is neither a necessary nor a sufficient criterion for homology identification. The cladistic approach is undoubtedly appropriated to discriminate between homology and homoplasy whenever similarity coincides with sameness, but it has little to offer in cases in which sameness and similarity do not co-occur (by the virtual absence of the latter).

An important limitation of the cladistic methodology, as far as it concerns to the homology problem, resides in its disregard in performing detailed, in-depth assessment of character hypotheses—namely primary conjectures of homology—beyond the test of congruence, which specifically does not deal with character analysis in itself (Rieppel and Kearney 2002: 59). The generalized adoption of such methodology by archaeological research oriented to investigate variation patterns in artifactual phenotypes, in some way precludes the implementation of a more sophisticated approach to the treatment of homology than that that is usually found in the current literature on the subject (Lycett 2010; O'Brien 2010). Just like in the case of biological systematics, what evolutionary approaches in archaeology need to develop is a sound methodology aimed to evaluate characters in terms of their developmental and/or functional causes (Rieppel and Kearney 2007; Rieppel 2008). Some ideas about the way to overcome present limitations in relation with this problem shall be discussed in the next sections of this paper.

TOWARDS AN INTEGRATIVE APPROACH IN THE STUDY OF HOMOLOGIES IN LITHIC ARTIFACTS: THE RATIONALE, THE STRATEGY, AND THE PROBLEMS

As recent theoretical developments in biological systematics suggest, a unified approach to homology—i.e. one integrating ontogeny and phylogeny into a single interpretive and operative framework (Laubichler 2000; Rieppel 2005; Wagner 2007; Wagner *et al.* 2007; Ereshefsky 2009)—represents a seemingly viable project aimed to address problems that neither the taxic nor the developmental approaches alone could satisfactorily solve (e.g., how to accommodate the multiple, and often competing perspectives and research agendas on homology?; how to provide solid causal grounding to our primary homology conjectures or character statements?; how to understand the phenomenon of hierarchical disconnect, i.e. the fact that non-homologous factors at one level can cause homologous traits at a higher hierarchical level and, conversely, homologous factors can cause nonhomologous characters?; Rieppel and Kearney 2007; Rieppel 2008; Ereshevsky 2009).

The main tenet of this paper is that in order to enlarge the framework for homology recognition and testing in evolutionary archaeology, it is crucial to engage in a synthesis similar to that is now ongoing in the field of biological systematics. It is significant to note that, although not directly addressing the problem of homology identification and validation, some scholars (Riede 2006, 2008; Shott 2008, 2010; Lycett 2010) have already started to call attention on the importance of integrating ontogenetic aspects of lithic and other artifacts (e.g., reduction sequences) with patterns of phylogenetic evolution, in order to get a better understanding of the evolutionary process underwent by such material entities. At present, however, the precise way in which the advocated synthesis may proceed is less than clear.

A fundamental step towards a unified approach to homology in the evolutionary study of artifacts should be, I would argue, to establish equilibrium between phylogenetic and character analyses since, as it was already mentioned, there is a marked trend to lay emphasis on the former at the expense of the latter. Homology hypotheses should be testable in other ways than just on the basis of inferred

monophyletic groups after the application of the congruence criterion (Rieppel and Kearney 2002: 63). The test of morphological characters can indeed be carried out using the main criteria of homology proposed in the early 1950's by the German systematist Adolf Remane: a) topological equivalence (criterion of 'sameness of position'), b) special quality of structures, and c) linkage by intermediate forms (Wenzel 1992: 369; Rieppel and Kearney 2002: 59). Topological equivalence, the first and foremost criterion of homology, is based on the idea that homologous structures share similar locations and connections with adjacent parts; special quality designates any single characteristic or trait contributing to the distinctiveness of a structure, in such a way that homologues tend to present the trait more likely than non-homologues; the existence of intermediate forms, finally, imply that homologous structures tend to be more similar early in ontogeny than later, owing to the fact that intensive evolutionary modification can cause a loss of morphological similarity of homologous structures in adult (i.e. fully functional) forms (Moczek 2008: 436-437). At the core of Remane's proposal lies a probabilistic approach to homology (Laubichler 2000: 780): a homology hypothesis increases in likelihood when more than one criterion is fulfilled. All these criteria are applicable to data coming from such disparate sources as comparative anatomy, comparative fossil anatomy, comparative embryology, comparative physiology and biochemistry, and comparative ethology (Wenzel 1992; Rieppel and Kearney 2002; Brigandt 2003), and deal—particularly the first and third—with the causal processes of ontogeny. And ontogeny matters because morphological homologues are complex structures that change through time (Griffiths 1999).

The endeavour of testing homology hypotheses concerning lithic artifacts would benefit from the systematic and comparative study of large collections of artifacts from archaeological contexts but, above all, from the comparative study of collections of experimentally produced tools and debitage. By means of replicative experiments (despite their potential pitfalls; see critical appraisals in Morrison 1994 and Koerner 2011), the ontogeny of lithic artifacts can be approached in an analytic way similar to that of developmental biology. An alternative to experimentation would be the use of ethnographic and ethnoarchaeological data about the life-histories of different artifact classes. However, it must be realized that there is a general paucity of ethnographic information about lithic tool production and use (Shott and Sillitoe 2005: 654). Moreover, while this kind of technology was still in use—at least occasionally—until recently (i.e. 1980's) in different regions around the world (e.g., Australia, Central America, Amazonia, Eastern Africa, and the New Guinea Highlands), it is virtually impossible nowadays to find people engaged in chipped stone production on a regular basis due to the massive adoption of metal tools and weaponry almost everywhere (Sillitoe and Hardy 2003: 555). This situation clearly hampers the implementation of an ethnoarchaeological approach to the subject.

Replicative experiments of specific lithic reduction sequences (Flenniken 1984; Whittaker 1994 and literature cited therein) possess the advantage of providing a good context, at a relative low cost, for the testing of homology hypotheses following the Remane's criteria in highly controlled conditions, allowing for the reiterative deployment of procedures and the statistical analysis of resulting data. It cannot be overemphasized, however, that the success of the proposed strategy depends on the resolution of a series of questions related to the process and pattern of artifactual phenotypic variation that are begging for a more clearer understanding than that is available today.

I would argue that a developmental approach to homology recognition and testing may represent a practicable undertaking only if it can be demonstrated that: a) the life-history of different artifact classes is capable of being assimilated—to a certain extent—to the biological concept of ontogeny in a relevant or not merely impressionistic way; and b) the artifactual phenotypes exhibit a certain degree of constancy (Waddington 1957) at the individual and population levels. In other words, it seems clear that only if lithic artifacts truly develop, and in a non-random or idiosyncratic fashion, an ontogenetic or developmental approach to homology is feasible. In the remainder of this section I shall briefly discuss these pressing issues.

The first problem that cries for clarification is the extent to which the concept of ontogeny is

relevant to describe the life-history of lithic artifacts. Ontogeny can be broadly defined as the history of structural change affecting a unity (whatever it may be), without the loss of the organization which allows that unity come to existence (Maturana and Varela 1987: 74). Ontogeny form part of the more general phenomenon of intarvariation, which consists in the internal variation of a system as a consequence of the instability of structural units over time (cf. Schreider 1960). Organismal units express such intravariation through the fundamental processes of growth, development, and senescence, all these being fundamental causal forces contributing to phenotype construction along life cycle. Phenotype construction, principally during its early phases, is inherently morphogenetic, with each event dependent on previous ones and contextualized by collateral ones (Salthe and von Sternberg 2009).

Lithic artifact production and use are reductive phenomena (Andrefsky 2005: 30, 34-38; Clarkson 2007: 32). This implies that the general process affecting most artifact classes (either tools or debitage) along their life-history trajectories (i.e. the succession of events extending "from the first flake removed from a core though any potential resharpening and usewear that occurs prior to final discard"; Lycett 2010: 227; see also Andrefsky 2009: 67) is decrease instead of growth (e.g., a biface cannot be bigger than the blank from where it was produced, becoming even smaller as the reduction sequence advances). This general statement, however, may not be true in all cases: e.g., unused flakes resulting from the reduction of a core or other artifacts do not undergo further decrease until discard, which can be immediate. The general norm of decrease or stability (either by sharpening, wear, or discard) in the life-history of lithic artifacts introduces a significant difference with the ontogeny of organismal units, which tend to grow by increase in the size and/or the number of components (Cameron 2002). A further discrepancy comes from the fact that organismal units undergo a process of increasing differentiation as growth progresses. Such differentiation involves diversification in the form, function and hierarchical organization of components. Clearly, lithic artifacts do not engage into a process of internal differentiation, at least in the same sense that cells, tissues or whole organisms do. Chipped stones are more like some hard components of the phenotype of certain organism (e.g., mollusk valves) in that they depend on the growth, differentiation, and maturity of other components of the phenotype in order to come into existence and achieve a definite form. Stone artifacts experience a sort of mechanical (as opposed to organic) differentiation, in the sense of becoming increasingly segmented (or at least susceptible of being segmented) into more or less identifiable parts (e.g., an endscraper as it is shaped into a piece with a sharp working edge, a proximal hafted end, and two lateral edges).

Another fundamental process contributing to morphogenesis is development. In general terms, development is progressive change, a process of fine-tuning enhancement through the differential promotion of latent informational constraints (i.e., sites or regions that might assume more than one configuration), followed by the ensuing fixation of some of such constraints (Salthe 2010: 358-359). The 'canonical developmental trajectory' of different systems (Salthe 1993) typically runs from immaturity (dominated by morphogenesis) through maturity (in which form is definitive for the kind of system) to senescence (in which form increasingly accumulates distorting marks as a result of interactions with the environment) (Salthe 2010: 60). Biological development—a phenomenon intimately associated with growth—is mainly conceived as the attainment of an increasing functional ability (maturity) along the ontogenetic process (Cameron 2002: 10), functional ability being measured in relation with some particular function or set of functions. Chipped stones (or at least some of them) 'develop' in the sense that they experience progressive change (i.e. decrease and shape modification). The question that arise, however, is if lithic tools really reach something like a mature (i.e. fully functional) or definitive form. On the one hand, from the perspective of the so-called 'teleological model' (Bleed 2001)—i.e. that embraced by the *châine opératoire* school as it was characterized by Dibble (1995), Bleed (2001), and Shott (2003)—reduction sequences are considered as more or less prolonged series of actions aimed to a somewhat predetermined goal or end-product, following a sort of mental template. From this standpoint, tools would really attain a mature stage in which their functional ability

or performance is the highest. On the other hand, the rival 'evolutionary model' (Bleed 2001) emphasizes the rather contingent and situational nature of lithic technology, understanding stone production as a continuous and "expanding array of alternatives defined by intervening options and outcomes" (Bleed 1991:20) which makes unlikely, in most cases, the existence of predictable end-results. Under this perspective, the very idea of a mental template is put into question (e.g., Bleed 2001; Davidson 2002; cf. Costa 2010), as it is the proposition of a clearly identifiable 'mature' stage in the life-history of most tools. This contentious issue is far from being resolved, but it seems prudent to assume that at least certain tools—likely those in which function and selection for performance impose very narrow constraints on form and morphogenetic process—indeed attain an state that could be properly considered as 'mature' immediately before the point of first usage, while other less functionally and morphologically less constrained tools change in a apparently undirectional way. I shall return later on this point when discussing the concept of 'canalization'.

Senescence or aging, finally, designates irreversible changes—assessed by means of specific biomarkers (Fox 2007)—in structure and function (generally involving impairment or loss of a function) of a whole organism or part of an organism that occur after maturity as a result of time-dependent processes (Medina 1996). It is an observational fact that lithic edges eventually become worn and blunt, then needing some amount of restoration for further use with the same or a closely related function (Andrefsky 2009). This is understood by some as representing senility or aging following first usage (Lycett 2010: 227 footnote nº 2; Shott 2010: 275). The indicators of such process (analogous to biomarkers) are usewear and resharpening. It must be noted that the strict application of the concept of senescence to stone tools is logically reliant on the acceptance—at least partially—of the tenets of the teleological model about lithic reduction. Tool must mature (i.e. to reach a definitive and fully functional form) in order to age. If tools do not mature, then they cannot age but simply change. Instances of tools that seems to fit well into the developmental model are most of the North American bifaces (e.g., projectile points), which go through a clearly differentiated production phase and through a subsequent use-life phase (i.e. the service life of one tool; Shott and Sillitoe 2005: 654) (Wilson and Andrefsky 2008: 87; Andrefsky 2009: 69). Examples of the entangled production-use model which implies a continuously changing form resulting from successive phases of use and resharpening are flake knives (Andrefsky 2009: 69), Australian endscrapers (Clarkson 2005), and most bifaces from areas of the world different than North America (Wilson and Andrefsky 2008: 87; cf. Clarkson 2002).

The second problem refers to the degree of constancy exhibited by those artifactual phenotypes that indeed develop. The concept of phenotypic constancy is linked to the notion of developmental homeostasis, i.e. "the ability of an organism to maintain a more buffered series of developmental pathways resulting in increased phenotypic uniformity of individuals in a population" (Etges 1989: 189). Developmental homeostasis ensures phenotypic constancy in the face of genetic, environmental, and developmental variation (Waddington 1957), and is controlled by two main processes: canalization and developmental stability (Debat and David 2001). Canalization designates the process by which phenotypic variation is reduced, at the population level, by developmental mechanisms (Stearns *et al.* 1995). Canalization buffers development to reduce the amount of variation potentially introduced by genetic and environmental factors, thereby ensuring phenotypic constancy in populations (Clarke 1998; Debat *et al.* 2000). Developmental stability, in turn, is the ability of an organism to maintain a stable development under a particular set of conditions due to the existence of mechanisms that reduce variability caused by accidents or random perturbations, i.e. noise (Clarke 1998; Van Dongen and Lens 2000). Canalization reduces phenotypic variation among individuals whereas developmental stability reduces variation within individuals (Etges 1989). The lack or low degree of homeostasis is called phenotypic plasticity (Etges 1989), which is defined either as the ability of a genotype to express different phenotypes across a range of environments (Liefting *et al.* 2009), or the ability of an organism to alter its physiology, morphology, and development in response to changes in the environment (Callahan *et al.* 1997). Phenotypic plasticity usually varies between habitats as a

function of the degree of spatio-temporal heterogeneity (Liefting *et al.* 2009).

We can expect that the possibility of approaching homologies in lithic artifacts by means of the study of developmental patterns at the individual and population levels, heavily depends on the degree of developmental homeostasis in the ontogeny of artifactual phenotypes: i.e. the lesser the degree of developmental homeostasis, and hence of phenotypic constancy, the lesser the chances of obtaining useful information about potentially homologous traits. Nevertheless, a proper assessment of the relative contribution of developmental homeostasis and phenotypic plasticity to the patterns of artifactual variation requires a deep understanding—and some degree of quantification—of the influences of informational (i.e. genetic, epigenetic, behavioral, symbolic; Jablonka and Lamb 2005) and environmental factors (including the interaction between both kinds of causes) on the expression of the artifactual phenotypes. At the present time we notoriously lack such understanding and analytical sophistication, so an agenda for further work on this subject should unavoidably include these critical topics.

CONCLUDING REMARKS

To enlarging the framework for homology recognition and testing at the level of artifactual phenotypes is a much relevant goal in evolutionary archaeology, as long as this field aspires to obtain a deeper understanding of evolution occurring at different levels along a hierarchy of entities and processes involving the human clade. Current emphasis on cladistics as the almost unique context in which homology hypotheses are formulated and tested should not hinder the exploration of other sources of information about homologous traits in lithic artifacts. In this vein, I advocated here for a more equilibrated approach to the homology problem, one integrating phylogenetic and ontogenetic perspectives into a coherent research program. However it must be realized that, in order to make of this project a viable effort, a great deal of knowledge about the many factors influencing the patterns of intervariation and intravariation in artifactual phenotypes ought to be achieved. Chief among the issues that need to be urgently addressed is the assessment and quantification of the differential contribution of those factors involved in the construction of artifactual phenotypes, namely the culturally inherited and cognitively processed information, the environment, and the interaction between both factors. In this sense, one major objective of evolutionary archaeology should be to identify the causes of the phenotypic variance and covariance within and between life-history traits in artifacts, as well as the relative contribution of such sources to the total phenotypic variance within each trait. This might aid to formulate explicit models about the way in which the phenotypic variance of artifactual traits can be partitioned. The second major problem to address is the evaluation of the degree of developmental homeostasis in the ontogeny of artifactual phenotypes, particularly of those artifact classes that undergo a true developmental process as it was defined above. The pertinence of an experimental program to attack the problem of homology recognition and validation in lithic artifacts seems to be contingent on the demonstration that, at least for certain artifact classes, the morphogenetic process is constrained to a certain degree, i.e. the amount of equifinality is relatively low. However, it has to be remembered that due to the phenomenon of hierarchical disconnect, even non-homologous developmental pathways can cause the same homologous morphology (Abouheif 1999; Ereshevsky 2009). All these problems deserve to be thoroughly investigated, both theoretically and empirically.

As a final thought, I want to mention that different authors (e.g., Binford 1968; Dunnell 1971, 1978) have stated that the terms we use to create our data directly establish a determination over the kind of operations or procedures that we can subsequently execute on those data. In this sense, it might be necessary to rephrase many of the linguistic expressions already in use in lithic analysis into terms or expressions usually employed in organismal evolutionary literature, after assessing for adequacy and relevance (e.g., life-history for ontogeny, standardization for canalization). This may aid to reduce ambiguity and imprecision in the communication of ideas and results but, above all, to set the problem in a proper and long-established frame of reference.

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